SWEDISH CONIFEROUS FOREST PROJECT

BARRSKOGSLANDSKAPETS EKOLOGI

TECHNICAL REPORT 9 1977

NUMBERS, BIOMASS AND RESPIRATION OF NEMATODA, ROTATORIA AND TARDIGRADA IN A 120-YEAR-OLD SCOTS PINE FOREST AT IVANTJÄRNSHEDEN, CENTRAL SWEDEN

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ISSN 0346-7708
ISBN 91 7544 309-0

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Abstract

Different groups of soil organisms were investigated in a monthly sampling programme from June 1974 to June 1975. This paper reports part of the results dealing with Nematoda, Rotatoria and Tardigrada. These animal groups were extracted by means of a modified Baermann-method. The results are given both on a gram basis for the different soil layers and on a m^2 basis including all layers down to 10 cm. The highest annual mean value was obtained in the S-layer with about 600 animals gdw^{-1} (biomass 21 µg dw), followed by the FH-layer 550 animals gdw^{-1} (13 µg dw) and the mineral soil 20-25 animals gdw^{-1} (0.8 µg dw). The total annual mean number per m^2 was about $6.0 \cdot 10^6$ (biomass 162 mg dw) of which the nematodes accounted for $5.4 \cdot 10^6$ (112 mg dw), the rotifers $5.8 \cdot 10^5$ (37 mg dw) and the tardigrades $6.0 \cdot 10^4$ (13 mg dw). All groups fluctuated rather much over the year with summer minimum ($1.3 \cdot 10^6$ animals/m^2) and winter maximum ($8.6 \cdot 10^6/m^2$) for the nematodes. For estimations of respiratory metabolism both the influence of size composition and field temperature were considered. The total annual oxygen consumption for all groups was about 2.5 l per m^2 corresponding to an emittence of 1.1 g carbon as carbon dioxide which is about 0.7 % of the input to the soil system. The nematodes used 2.0 l oxygen corresponding to a carbon emittence of about 0.5 % of the input.

1. Introduction

A certain amount of the carbon and nitrogen in the soil is incorporated in the biomass of the soil organisms. The rate of turnover of these biomass-bound elements differs with the kind of organisms and is also influenced by biotic interactions, climatic conditions and inputs of energy and nutrients from the above-ground system. To elucidate the fluxes of carbon and nitrogen through different groups of soil organisms in a coniferous forest soil an extensive sampling program including all groups of soil organisms except the protozoans was undertaken. For the animals it was suggested that the conventional way of estimations of numbers, biomass and respiration as outlined by workers as O'Connor (1963) and Healey (1967)

would provide a basis for calculation of the fluxes of carbon and nitrogen through the populations. The aim of the present paper is to present a part of this study including estimations of number, biomass and respiration of the metazoan microfauna. The concept microfauna here refers to nematoda, rotatoria and tardigrada.

Few studies have been made of members of the metazoan microfauna in coniferous forest soils and no extensive investigation of these organisms from Swedish forests has so far been published. From Finland the studies by Huhta and Konskenniemi (1975) include nematoda, rotatoria and tardigrada and the works by Nielsen (1949), Bassus (1962) and Wasilewska (1971) deal with nematodes from more central European conditions.

Some of the data presented in this paper will later be used to construct a conceptual model of the carbon and nitrogen fluxes between different groups of soil organisms and the non-living parts of the system.

2. The site

The investigation was undertaken in a 120-year-old stand of Scots pine (*Pinus silvestris*) at Ivantjärnsheden, Jädraås (Ih VA) in Central Sweden ($60^{o}49'$N and $16^{o}30'$E 185 m above sea level). The study area, the composition of the vegetation and the soil conditions have been described in a number of reports (Bråkenhielm 1974, Bringmark & Petterson 1975 and Popovič 1976). The following description is taken from Bråkenhielm (1974): "The forest is of Cladonio-Pinetum boreale (Cajander 1921) type. According to Arnborg (1953) it can be classified as very dry to dry dwarf shrub type. It consists of a mature pure pine stand with occasional, severely suppressed spruce. It was self-sown in the 1850s. Thinning by removal of weak trees was done in 1962. *Calluna vulgaris* is thin, mosses and reindeer lichens are abundant. The latter also forms patches with a diameter of 10-20 m." The FH-layer has a thickness of 2.6 ± 0.3 cm. The mineral soil consists of sand sediment of glacifluvial origin. The pH of the FH-layer is 3.8 - 4.6 (Popovič 1976) and the C/N quotient is about 47 (Bringmark and Petterson 1975). The mean values of organic material (% loss of ignition) obtained by M. Clarholm, E. Bååth & B. Söderström (pers. com.) were: S-layer 95.5 %, FH-layer 73.4 %, A_2 horizon 3.44 % and B horizon 4.25%. The longterm mean annual temperature in the area is 3.8^{o}C and the mean annual precipitation 607 mm.

3. Methods

3.1 Sampling

The samplings were coordinated with those for micro-organisms and other soil fauna groups. Six core samples were taken on about the 20:th each month (except January and March 1975) from June 1974 until June 1975 in fixed sampling places randomly located over the 100 x 200 m field plot. The cores (diam 2.3 cm) penetrated from the surface of the humus layer down to a depth of 10 cm. They were transferred to plastic tubes (Cerbo diam 26 mm length 65 mm), placed in a cold bag and transferred to Stockholm for extraction the next morning.

3.2 Extraction

Before extraction the cores were sliced into four parts. These were the litter or S-layer, the humus or FH-layer (average depth 0-2.6 cm) and two mineral parts referred to as "M_1" and "M_2"-layer. The M_1 -layer (average depth 2.6 - 5.9 cm) included the bleached layer (A_2) and the M_2 (average depth 5.9 - 10 cm) generally included the uppermost part of the illuvial B horizon. The animals were extracted by means of a modified Baermann method. Nylon net sieves with plastic rims (diam 75 mm, mesh size 1 mm) were used which fitted into the glass funnels (10 cm diam). A fliselin filter was used. Fliselin has about the same structure and porosity as the Ederol 261 filter papers recommended by Seinhorst (1962). Small subsamples about 3 ml in volume were spread in a thin layer over the sieves and placed in the water-filled funnels. Batteries with funnels were arranged as in Fig. 1. After six hours, electric bulbs (25 W) over the funnels were switched on and the temperature in the samples increased to about 28 - 29^{o}C. After about 20-24 hours the extraction was finished and the animals were killed by heat and stored in 4% formaldehyde. The dry weight of the soil on the filters was determined after extraction.

3.3 Counting

Before counting, the suspensions with the animals from each soil layer were pooled into two batches originating from three cores each. Thus from each sampling occassion eight countings 2 x 4 (the four horizons) were undertaken. Each time the material from the same three sampling stations were poured together. The total animal number was counted in counting dishes under low magnification (40 x). To concentrate the animal suspensions after counting these were transferred to 15 ml centrifugal

tubes. For identification and biomass determinations the concentrated suspensions were then examined on a watch glass under higher magnification (125-200 x). About 150-200 nematodes and varying numbers of rotifers and tardigrades from each layer were examined.

3.4 Biomass

The biomasses were determined by means of volumetric methods. The method of Andrassy (1956) was used for nematodes and for tardigrades the method of Hallas & Yeates (1972). A special method for estimations of rotatorian biomass was developed. From weights of camera lucida drawn projections of a number of rotifers, their volumes and weights were determined assuming a density slightly over 1. Length weight regressions were calculated for the most frequent categories of nematodes and for the rotifers (Table 2). Table 2 also includes the mean individual fresh weights of animals obtained on all the eleven sampling occasions. The nematoda and rotatoria are assumed to have a dry weight of 20% and the tardigrada 25% of the fresh weight.

Individual mean biomasses of the categories listed in Table 2 were calculated for each month, and when these values were multiplied by the appropriate monthly mean density they provided estimates of the mean monthly biomass.

3.5 Ancilliary measurements

Extensive temperature data have been collected by the meteorological research group, as described in Lindroth and Perttu (1975). Soil temperatures were measured at various depths and registered with a Grant recorder. During the period 740611-740813 the recorder was out of order. The values from this period have been obtained from Popovič (1976). For the purpose of estimating the respiratory activity of the animals the monthly mean soil temperature at 5 cm below the surface was selected (Table 1 and Fig. 9 G).

Most of the water content values were determined by gravimetrical methods on each sampling occasion by M. Clarholm. In the values from the end of the period determinations by E. Bååth, P-E. Jansson and B. Söderström are included (Table 1 and Fig. 9 H).

3.6 Annual mean values

The annual mean values of number, biomass and respiration were calculated in two steps. First the seasonal mean values were calculated starting

with the summer of 1974 (June-August), the autumn of 1974 (September-November), the winter of 1974/75 (December and February) and ending with the spring of 1975 (April and May). From these four seasonal mean values the annual mean value was estimated. Thus June 1975 was not included. Due to the relatively few sample units on each sampling occasion (6) these seasonal values give a better estimate of mean number as they are made up of 12-18 sample units each. The total number of sample units behind the annual mean values is thus 60.

4. Results

4.1 Number and biomass

The numbers of the different animal groups per gram soil can be seen in Table 3 and Figs. 1-3. In all layers the nematodes constituted the greatest part of the metazoan microfauna (77-95 % of the mean annual values). The relative frequency of the rotifers was greatest in the M_1- and M_2-layers (17-22 % of the fauna). The tardigrades made their greatest contribution to the fauna in the S-layer (4.1 % of the fauna) while they only occurred in very low numbers in the mineral soil (0.4 % of the total number).

The mean values for all animal groups fluctuated rather widely, especially in the S- and FH-layers (Figs. 2-4).

In the S-layer the highest number of nematodes was obtained during November and December, while their highest number in the FH-layer was found in February. In the mineral soil the fluctuations were much smaller and could not so clearly be related to the season.

The values for the rotifers fluctuated to some extent in another way (Fig. 2). In the S-layer peak numbers were found during June and December. In the other layers increased numbers were obtained during November, April and June.

The tardigrade number also fluctuated in its own way and high numbers in the S-layer occurred in July, November and May. Very few tardigrades were found in the mineral soil but they occurred more frequently in samples from these layers during the colder part of the year which might indicate a downward migration.

The mean individual biomass for the total fauna and the different animal groups can be seen in Fig. 5. The pattern is somewhat different for the three animal groups. Thus for nematodes the lowest biomass values were obtained in October and February and the highest in July and April. The rotifers had lower values from July to October and higher and increasing values from November to April. The tardigrades did not fluctuate very much but showed lower values during November and December. There were no very great changes in mean individual biomass and the max/min ratio for nematodes was 1.9, for rotifers 2.1 and for tardigrades 2.9.

Number and biomass of the total fauna are shown in Table 4. The fluctuations in number largely follow those of the nematodes (Fig. 2). Comparing the mean annual numbers and biomasses (Table 4 bottom) it is evident that the highest values were obtained in the S-layer followed by the FH-layer. Much lower values were found in the mineral layers. However if we compare the values per gram organic material (Table 5) these differences disappear almost completely and the highest values of number and biomass were found in the M_1-layer.

Table 6 and Fig. 6 show number and biomass per m^2. The nematodes constituted about 89 % of the micro-fauna (mean annual number $5.4 \cdot 10^6/m^2$), the rotifers about 10 % ($5.8 \cdot 10^5/m^2$) while the tardigrades only made up about 1 % ($6.0 \cdot 10^4/m^2$) of the total number. If we compare biomass values the relative proportions of the different groups will be somewhat altered because tardigrades and rotifers generally are heavier than nematodes (Table 2). Thus the annual mean dry weight of the entire fauna was 162 mg/m^2 of which the nematodes made up 112 mg or 69 %, the rotifers 37 mg or 23 % and the tardigrades 13 mg or 8 %.

The biomass curves fluctuated in a slightly different way to the curves for numbers (Fig. 6) which in all groups might indicate an increased requitment during the autumn. This is indicated by the lower mean individual biomass values during this period (Fig. 5). The highest biomass values for all three groups were obtained during April.

The fluctuations in both numbers and biomass were quite strong for all groups. A measure of this is the quotient between the highest and lowest value obtained (ratio max/min in Table 6). The highest quotient

was obtained for the tardigrades (14.6 for number and 15.4 for biomass). For nematodes and rotifers this quotient varied between 5.6 and 9.8.

4.2 Number and biomass of nematode groups

The mean annual values for number and biomass of different nematode species and genera can be seen from Table 7. When the population density was considered species belonging to *Acrobeloides*, *Plectus*, *Tylenchus* and *Aphelenchoides* dominated. However when considering the biomass the dominant genera were *Plectus*, *Eudorylaimus*, *Aporcelaimus* and *Acrobeloides*.

The food sources and the classification of nematodes into different feeding groups have been widely studied and discussed. As pointed out by Wasilewska (1974), our knowledge of the area is still insufficient. However it may still be convenient to make a rough feeding ecological classification. Thus in the present study the fauna was divided into three feeding ecological groups, *viz.*, root/fungal feeders, bacterial feeders and miscellaneous feeders. No obligate predators such as the members of *Mononchoidea* were found.

The food sources for the root/fungal feeders are fungal hyphae or roots. Most probable as root feeders are *Tylenchus* and *Tylenchorhynchus*. Members of *Ditylenchus*, *Aphelenchoides* and *Tylencholaimus* have been observed to feed on fungi (Sohlenius *et al.* 1977) but some species belonging to these genera might also feed on roots.

Many of the species are classified as bacterial feeders and members of many of the genera included in this group have been observed to feed on bacteria under laboratory conditions. The food sources of *Monhystera*, *Prismatolaimus*, *Achromadora* and *Alaimus* are however somewhat uncertain. Banage (1964) suggested that they should be included in the microbivorous group. However soil algae should be considered as a possible food source for a genus such as *Achromadora*.

The miscellaneous feeders include species which are rather poorly known with respect to their food sources. They have been observed to feed on soil algae and other soil animals. Members of *Eudorylaimus* and *Aporcelaimus* from the locality have been observed to feed on other nematodes on soil agar plates.

Numerically the bacterial feeders were the dominating group in all layers (Table 8, Fig. 7). Their mean annual population densities were 50-58 % whereas the root/fungal feeders accounted for 33-43 % and the miscellaneous feeders for about 6-10 % of the total nematode number in the different layers.

The curves for the population densities of the different groups in the different layers did not follow each other very well (Fig. 7). In the S-layer all the nematode groups reached their highest numbers during the autumn, whereas the conditions in the other layers was somewhat more varying. In the FH-layer very high numbers occurred during the winter. Tendencies to spring and autumn peaks could be seen in the mineral layers.

From the mean annual values per m^2 (Table 9) it is evident that the bacterial consumers accounted for 57 % ($3.04 \cdot 10^6$), the root/fungal feeders for 37 % ($1.96 \cdot 10^6$) and the miscellaneous feeders for only about 7 % ($0.37 \cdot 10^6$) of the total nematode number. However, if the biomasses are considered the relative proportions will be quite different with 44 % for bacterial feeders, 42 % for miscellaneous feeders and only about 14 % for the root/fungal feeders.

Both the root/fungal feeders and the bacterial feeders increased comparatively late in the autumn (Fig. 8), with peaks in December for root/fungal feeders and in February for bacterial feeders. The peak number of the miscellaneous feeders was obtained already in September. All three groups decreased rather rapidly during the spring (between April and May).

4.3 Respiration

For estimations of respiration the relation between weight and oxygen consumption described by Klekowsky *et al.* (1972) was used. It was also assumed that this equation could be used for rotifers and tardigrades owing to their related size and structure. For nematodes and rotifers the material from each month was divided into 10 weight classes on a logarithmic scale. The mean weight in each size class was used for calculation of oxygen consumption (Table 10). With knowledge of the relative weight class composition (Table 11 and 12) and animal number (Table 6 and 9) respiration at $20^{o}C$ was calculated. For tardigrades the respiration was calculated for each measured specimen.

For adjustment to field temperature the monthly mean temperature at a depth of 5 cm was used (Table 1). It has been shown that the relation between temperature and respiration for nematodes in several cases follows Krogh's curve (von Brandt 1960). Within the interval 0-15°C this has a Q_{10} value of about 3.95 which was used at a temperature correction factor for all animal groups. The respiration values were first recalculated to 10°C using a Q_{10} of 2.52 (valid for the interval 10-25°C). At temperatures below zero the Q_{10}-values can be assumed to be very high (20-50) according to Scholander *et al.* (1953a) and for the values slightly under 0°C (February -April) a Q_{10} value of 20 was used. No samplings were undertaken in January and March, thus the respiration values estimated for these months are based upon interpolated biomass values.

The rate of respiration for the different animal groups can be seen on Table 13 and Fig. 9. The curves for the different nematode groups (Fig. 9 D-F) were quite similar and all groups reached their highest metabolic activity during September. The curves for rotifers (9b) and tardigrades (9c) were quite different with peaks for rotifers during June and for tardigrades during July and May.

The total amount of oxygen consumed by all the animal groups during the year (Table 14) was about 2.5 l/m^2, of which the nematodes used up about 2.0 l (80%). For transfers to energy units the value of 4.775 cal per ml O_2 (Heilbrunn 1947) corresponding to 19.979 J was adopted. The amount of carbon liberated as CO_2 was calculated as described in Persson (1975). In Table 14 the figures for the corresponding amount of energy dissipated and carbon emitted as CO_2 are given.

5. Discussion

The obtained values of number and biomass should naturally be considered as minimum values. This is evident for two reasons. First it is probable that not all specimens were extracted by the method used, and secondly, the samples were only taken down to 10 cm below the litter layer. The Baermann-method in its original form obviously gives a rather poor result (Oostenbrink 1971). However modifications in the direction used in this study have increased extraction efficiency considerably (Nielsen 1947, Winslow 1964, Banage 1966). Nielsen (1948) obtained very good recoveries ("at least 90 %") for nematodes and rotifers, but did not consider his method so good for tardigrades. IBP-studies also provide

evidence that the highest recoveries have been obtained by workers who have used similar modifications of the Baermann-method (Petersen in prep.).

In a study on a Polish mixed pine forest locality on sand, Wasilewska (1974a) found quite considerable number of nematodes below a depth of 10 cm. It can be reasonable to assume that the obtained m^2 values in the present study should be increased by at least 20-30 % to compensate for inefficient extraction and for the part of the fauna that occurred below 10 cm.

The fluctuations in number and biomass were very pronounced, especially within the S- and FH-layers. It may be reasonable to consider the degree to which these fluctuations are real and the degree to which they are results of insufficient number of sampling units. From Figs. 1 and 2 it seem quite evident that the two pooled values (triangles and squares in the figure) from each sampling occasion follow each other quite closely, indicating real fluctuations. For the tardigrades the values are much more scattered, indicating a less satisfactory estimation of these animals due to their lower number and more clustered distribution. If the m^2 transferred values are considered (Fig. 6), a rather good agreement for the pooled values is obtained for the total fauna and for nematodes and rotifers alone whereas the values for the tardigrades also here are much more scattered.

Naturally it is not convenient to make any thorough generalisations on seasonal dynamics from just one year of samplings. However, it is interesting to notice that the nematode fauna fluctuated in quite a similar way in Finnish coniferous forests (Huhta *et al.* 1967). Also in these forests there were rather rapid decreases in numbers during the months of April and May, which occurred every year during this 3-year study. The Finnish workers discussed possible causes of their high winter recoveries. They were of the opinion that this was an artefact caused by an increased hatching of eggmasses when the samples were transferred to the warmer conditions in the laboratory, as it took a few days before the samples were extracted. Whatever the cause might be it is interesting to observe that the same winter increase in number occurred in the Swedish material in spite of a different extraction method.

Huhta *et al.*(op. cit.) used the Seinhorst elutriation technique, which in its initial stage is a mechanical method. The Finnish authors also discussed the cause of the decline during the spring and summer but only from a physical point of view and considered it to be a result of the dryer conditions during that season. The Swedish site also suffered from very dry conditions during the summer (Fig. 9h), which could be related to the lower density of the metazoan micro fauna during this season. However it should be kept in mind that the nematode number is probably highly influenced by predation. The microarthropods among, which most predators on the metazoan microfauna are found, certainly have higher tolerance for dryer conditions than the more water-bound members of the microfauna. The situation might well be that the balance between predation rate and rate of nematode requitment is such that there will be a net decrease during warm and dry conditions and a net increase during wet and cold conditions.

The influence of biotic relations on population dynamics has probably been too little considered by soil zoologists and soil microbiologists and, as Arpin (1975a and b) has suggested, a multiplicity of factors - both abiotic and biotic - certainly interact to govern seasonal changes in numbers.

As discussed by Huhta and Koskenniemi (1975) the accuracy of the estimates in studies like the present one decreases rapidly from densities through biomasses to community respiration. The use of $Q_{10}=2$ as was done by Huhta and Koskenniemi (1975) and Persson (1975) might give an overestimation and especially the winter values will be unreasonably high. It is quite possible that the closer use of Krogh's curve is more relevant as this shows higher and increasing Q_{10} values with lower temperatures. A tendency of higher Q_{10} values with lower temperatures seems to be a common feature among invertebrates (Scholander *et al.* 1953b).

The weight specific respiratory values obtained in the present study are high when compared with those obtained by Phillipson *et al.* (1977). These authors give values of about 0.45 ml O_2 $g^{-1}h^{-1}$ at 10^oC which could be compared with the values 0.84-1.10 ml O_2 $g^{-1}h^{-1}$ at 10^oC obtained in the present study. This is due to the fact that in the present study the relations between size and respiration, as described by Klekowsky *et al.* (1972), were considered. The Polish authors have shown that there is a strong increase in weight specific respiration with decreasing size of

the animals (cf. Table 10). Phillipson *et al.* (1977) and several other authors have used Nielsen's (1949) value of 1 l O_2 $kg^{-1}h^{-1}$ obtained for quite heavy nematodes. Therefore estimations by Phillipson *et al.* (1977) are most probably underestimations, as might be the case with several other studies.

It is doubtful whether it is correct to use estimations on respirations from nematodes on rotifers and tardigrades. However the values of $1.5\text{-}2.8 \cdot 10^{-3}$ l O_2 h^{-1} $ind.^{-1}$ for tardigrades estimated by this method are not far from the value $1.0 \cdot 10^{-3}$ l O_2 $h^{-1}ind.^{-1}$ obtained by Pigon & Weglarska (1953).

It should be remembered that even if the estimation of respiratory metabolism in the present study as well as in other similar studies are fairly uncertain it is most likely that they are underestimations. This is due to the rather exponential relation between temperatures and metabolism. Thus, as pointed out by Solhöy & Skartveit (1975), the use of monthly mean temperatures for temperature corrections tends to give underestimations.

Only few studies have been published so far on number, biomass and respiration of the metazoan microfauna in coniferous forest sites. However rather extensive studies have been undertaken in Finland by Huhta *et al.* (1967), and Huhta & Koskenniemi (1975). In the latter paper the more relevant part of these studies are presented even though, in this study, samples were only taken in the litter and humus layer during a period from May to September-October. Values were presented for nematode number ($1.1\text{-}1.4 \cdot 10^6$), biomass (36-45 mg dw/$m^2$) and respiration (0.33-0.73 l O_2/m^2) which were all much lower than those obtained in the present study (Table 14). The tardigrade number ($42\text{-}48 \cdot 10^3$) was quite similar to the Swedish one (Table 14) while the rotifers number ($29\text{-}32 \cdot 10^3$) was more than 10 times lower. The latter might partly be an effect of the large number of rotifers in the mineral soil as this layer was not included in the Finnish study. The values for nematodes estimated by Marshall (1974) in a Douglas fir plantation in British Columbia ($1.3 \cdot 10^6/m^2$) are fairly similar to the Finnish values. Wasilewska (1971) also found lower numbers and biomass values in an old Cladonia-Pinetum community. However, values quite similar to those from Ivantjärnsheden were obtained in younger succesional stages.

The obtained individual biomass values for the nematodes are in line with some recent results, *e.g.* those by Wasilewska (1971) and Phillipson

et al. (1977). It seems as if the general trend is that the individual mean nematode biomass in coniferous forests is lower than in other types of ecosystems (Petersen in prep.), which has also been pointed out by Nielsen (1949). Yeates (1973) gives a detailed list of biomass of different nematode species obtained from a beech forest soil. In general his values are higher than those obtained in the present study, which also indicates the prevalence of small specimens in the pine forest soil.

The nematode number and faunal structure closely resemble that found in an adjacent 15-20 year old stand (Sohlenius *et al.* 1977). In both age stages of forests there was a dominance of bacterial feeders. A similar structure was also found in a Polish Cladonio Pinetum community (Wasilewska 1971). Wasilewska found quite large fluctuations in number and biomass in this site. However, in contrast to the result of the Finnish and Swedish studies, there was a quite pronounced decline during the winter (February). Phillipson *et al.* (1977) found quite small fluctuations with increrased numbers during the early winter (December) in an English beech forest. This is in contrast to the result by Yeates (1972) who found decreases in number related to decreases in temperatures during the winter in a Danish beech forest.

The amplitude of fluctuations was rather great in the present study with about a seven-fold difference. This is rather a high value when compared with Phillipson *et al.* (1977) who found two-fold changes and Berge *et al.* (1973) who demonstrated a three-fold difference, while Banage (1966) and Yeates (1972) found a five-fold change. It is more in line with Huhta & Koskenniemi (1975) who found a six-fold difference in a Finnish spruce forest. Possibly this reflects more unstable conditions in the more northern coniferous forests when compared with the more southern deciduous forests.

The estimated value for the annual heat dissipation by respiration of the nematodes (9.8 kcal/m^2) is high when compared with results obtained in other similar studies . Thus the Finnish sites gave values of 1.6-3.7 kcal/m^2 and Wasilewska (1971) obtained 6 kcal/m^2 in a Polish pine stand.

A preliminary estimation of the carbon input to the soil system gives a value of 163.6 g carbon per m^2 and year. If compared with the figures in Table 14 it is evident that the total metazoan microfauna respired away about 0.67 % and the nematodes about 0.54 % of the added carbon.

6. Acknowledgement

I am very grateful to all colleagues within the project who have supplied data and made this study possible. The sampling programme was organized by Tryggve Persson who also contributed with valuable discussions and suggestions. Most of the population estimations and different calculations were done by Åsa Linder and Ingegerd Sohlenius.

Table 1. Monthly values for temperature, water contents and snow cover in Ih VA. Mean temperatures are obtained at a depth of 5 cm. Figures for water contents are given as percentages of the dry weight. At field capacity in the FH-layer the water contents are about 260%.

Month	Mean temperature at 5 cm °C	Water contents in the FH-layer in % of dw	Snow cover mean thickness in cm
1974			
June	10.7	52	-
July	12.0	111	-
August	11.5	171	-
September	11.5	184	-
October	5.0	275	-
November	2.1	188	0
December	0.5	242	9
1975			
January	0.1	643	11
February	- 0.8	548	15
March	- 1.6	n.d.	0
April	- 1.3	782	0
May	5.6	221	-
June	10.0	134	-

n.d. = not determined

Table 2. Individual mean live weight biomass of animals obtained from 11 sampling occasions and the relationship between body length (μm) and live weight biomass (W) (μg). The relationship is of the form: $L = b\sqrt[3]{W} + a$

Animal kind	Mean live weight (μg)	b	a	r
Tardigrada	0.887	-	-	
Rotatoria	0.317	$2.59 \cdot 10^{-3}$	$24.76 \cdot 10^{-2}$	0.79
Nematoda	0.099	-	-	
Root feeders	0.023	-	-	
Root/fungal feeders	0.053	-	-	
Bacterial feeders	0.081	-	-	
Miscellaneous feeders	0.625	-	-	
Tylenchus spp.	0.019	$0.73 \cdot 10^{-3}$	$4.55 \cdot 10^{-2}$	0.86
Tylenchorhynchus sp.	0.468	-	-	
Ditylechus spp	0.040	$0.70 \cdot 10^{-3}$	$5.31 \cdot 10^{-2}$	0.92
Aphelenchoides	0.018	$0.86 \cdot 10^{-3}$	$2.75 \cdot 10^{-2}$	0.99
Tylencholaimus mirabilis	0.218	$0.76 \cdot 10^{-3}$	$15.73 \cdot 10^{-2}$	0.95
T. stecki	0.424	-	-	
Rhabditis spp.	0.050	-	-	
Bunonema spp	0.041	-	-	
Acrobeloides sp.	0.095	$1.24 \cdot 10^{-3}$	$7.90 \cdot 10^{-2}$	0.94
Cervidellus sp.	0.067	-	-	
Teratocephalus spp.	0.017	$0.79 \cdot 10^{-3}$	$-0.008 \cdot 10^{-2}$	0.86
Euteratocephalus crassidens	0.015	-	-	
Plectus parietinus	0.148	$1.22 \cdot 10^{-3}$	$-3.40 \cdot 10^{-2}$	0.97
P. longicaudatus	0.095	$1.21 \cdot 10^{-3}$	$-6.54 \cdot 10^{-2}$	0.95
Chronogaster sp.	0.047	-	-	
Wilsonema sp.	0.050	$1.24 \cdot 10^{-3}$	$3.38 \cdot 10^{-2}$	0.87
Monhystera sp.	0.024	$0.82 \cdot 10^{-3}$	$5.55 \cdot 10^{-2}$	0.82
Prismatolaimus sp.	0.038	$0.64 \cdot 10^{-3}$	$4.06 \cdot 10^{-2}$	0.93
Achromadora	0.098	-	-	
Alaimus sp.	0.039	-	-	
Eudorylaimus spp.	0.330	$0.69 \cdot 10^{-3}$	$12.22 \cdot 10^{-2}$	0.93
Aporcelaimus sp.	2.121	$0.65 \cdot 10^{-3}$	$20.68 \cdot 10^{-2}$	0.98
Dorylaiminae odeff.	0.727	$0.62 \cdot 10^{-3}$	$24.20 \cdot 10^{-2}$	0.96

Table 3. Number of Nematoda (Nem.), Rotatoria (Rot.) and Tardigrada (Tard.) in different soil layers in Ih VA. Figures show number of animals g^{-1} dry soil.

Month	S-layer			FH-layer 0-2.6 cm			Mineral soil M_1, 2.6 - 5.9 cm			Mineral soil M_2, 5.9 - 10 cm		
	Nem.	Rot.	Tard.	Nem.	Rot.	Tard.	Nem.	Rot.	Tard.	Nem.	Rot.	Tard.
1974												
June	111	123.9	12.9	64	16.6	0.3	9.3	7.8	0	9.3	7.8	0.03
July	336	27.5	27.9	333	10.6	5.5	12.7	1.4	0	5.6	2.1	0
Aug.	239	17.2	2.5	204	5.2	0.4	12.5	2.3	0	22.9	3.3	0.1
Sept.	763	73.3	17.6	559	26.2	1.0	23.8	2.7	0	9.1	2.2	0
Oct.	447	29.2	19.5	457	17.1	2.5	17.0	2.0	0	10.3	3.8	0
Nov.	1041	73.6	35.0	534	33.1	3.6	27.9	10.9	0.1	18.4	6.1	0.2
Dec.	1116	108.2	29.3	801	29.3	15.3	36.1	1.4	0.1	16.6	3.4	0.1
1975												
Feb.	435	43.3	21.6	940	22.2	4.2	23.6	4.9	0.2	26.7	2.2	0.1
Apr.	524	52.9	27.0	754	46.7	8.2	26.3	8.3	0.2	33.5	13.8	0
May	278	25.6	48.1	214	8.0	3.6	18.9	3.2	0.4	11.0	3.3	0
June	274	78.5	9.8	150	12.0	0.2	25.2	9.7	0.1	18.1	1.6	0
Summer (74)	229	56.2	14.4	200	10.8	2.1	11.5	3.8	0	12.6	4.4	0.04
Autumn	750	58.7	24.0	517	25.5	2.4	22.9	5.2	0.03	12.6	4.0	0.1
Winter	775	75.8	25.5	871	25.8	9.8	29.9	3.2	0.2	21.7	2.8	0.1
Spring	401	39.3	37.6	484	27.4	5.9	22.6	5.8	0.3	22.3	8.6	0
Annual mean	539	57.5	25.4	518	22.4	5.1	21.7	4.5	0.1	17.3	5.0	0.1
Ratio max/min	10.1	7.2	19.2	14.6	9.0	76.5	3.9	7.8		5.9	8.6	
Frequency %	86.7	9.3	4.1	95.0	4.1	0.9	82.5	17.1	0.4	77.2	22.3	0.4

Table 4. Number and biomass of metazoan microfauna (Nematoda, Rotatoria and Tardigrada) in Ih VA. Figures show number of animals g^{-1} dry soil (no) and dry weight biomass in $\mu g\ g^{-1}$ dry soil (biomass).

Month	S-layer		FH-layer 0-2.6 cm		Mineral soil M_1 2.6-5.9 cm		Mineral soil M_2 5.9-10 cm	
	no	biomass	no	biomass	no	biomass	no	biomass
1974								
June	248	13.3	81	2.7	17	0.7	17	0.7
July	391	17.5	349	10.6	14	0.4	8	0.3
Aug.	259	5.3	210	3.8	15	0.3	26	0.6
Sept.	854	23.8	586	13.3	27	0.6	11	0.3
Oct.	495	12.5	477	8.5	19	0.4	14	0.3
Nov.	1150	32.0	570	13.8	39	1.3	25	0.8
Dec.	1254	32.5	846	19.2	38	0.8	20	0.6
1975								
Feb.	499	14.1	966	16.2	29	0.7	29	0.6
Apr.	604	27.3	808	27.8	35	1.5	47	2.2
May	352	20.7	226	7.0	23	0.8	14	0.5
June	362	14.8	162	3.6	35	1.1	20	0.4
Summer (74)	299	12.0	213	5.7	15	0.5	17	0.5
Autumn	833	22.8	545	11.9	28	0.8	22	0.5
Winter	877	23.3	906	17.7	33	0.8	25	0.6
Spring	478	24.0	517	17.4	29	1.1	31	1.3
Annual mean	622	20.5	545	13.2	26	0.8	22	0.7

Table 5. Annual mean number and dry weight biomass of metazoan microfauna in different soil layers per gram organic material.

Category	S-layer	FH-layer	Mineral soil M_1-layer	Mineral soil M_2-layer
Total number	651	743	765	527
Total biomass µg	21.5	18.0	22.5	16.8
Nematoda no	564	705	631	407
Rotatoria no	60	31	131	118
Tardigrada no	27	7	3	2

Table 6. Number and biomass of Nematoda, Rotatoria and Tardigrada per m^2 in the uppermost 10 cm of the soil in Ih VA. Figures show number of animals in thousands m^{-2} (No 10^3) and dry weight biomass in mg m^{-2} (Biomass).

Month	Nematoda		Rotatoria		Tardigrada		Total	
	No 10^3	Biomass	No 10^3	Biomass	No 10^3	Biomass	No 10^3	Biomass
1974								
June	1 261	33	818	48	13	3	2 092	84
July	3 157	82	225	11	58	15	3 440	108
Aug.	3 003	53	273	11	9	2	3 285	65
Sept.	5 531	117	425	19	20	5	5 976	141
Oct.	4 426	71	377	15	32	7	4 835	93
Nov.	6 144	131	940	57	63	10	7 147	198
Dec.	8 177	150	479	31	132	22	8 787	203
1975								
Feb.	8 570	124	454	32	56	12	9 080	169
Apr.	7 812	223	1 265	104	82	24	9 159	352
May	2 797	74	335	19	75	19	3 207	112
June	2 764	50	560	36	12	6	3 337	93
Summer June-Aug. (74)	2 473	56	448	23	27	6	2 948	85
Autumn Sept.-Nov.	5 368	106	581	30	40	8	5 989	144
Winter Dec. & Feb.	8 377	137	469	32	96	19	8 942	187
Spring April-May	5 306	149	807	62	79	21	6 192	232
Annual Mean value	5 380	112	578	37	60	13	6 018	162
Ratio max/min	6.8	6.8	5.6	9.8	14.6	15.4	4.4	5.2
Rel. prop. %	89.4	69.1	9.6	22.6	1.0	8.3		

Table 7. Number and biomass of nematodes per m^2 in the uppermost 10 cm of the soil in Ih VA. Figures show annual mean number of animals in thousands m^{-2}. dry weight in mg m^{-2} and percentage of total nematode number and biomass.

Category	Number		Biomass	
	no 10^3	%	mg dw	%
Root/fungal feeders				
Tylenchus	885	16.3	3.2	2.8
Tylenchorhynchus	11	0.2	0.9	0.8
Ditylenchus	199	3.7	1.6	1.4
Aphelenchoides	723	13.3	2.7	2.4
Tylencholaimus mirabilis	135	2.5	5.1	4.6
T. stecki	24	0.4	2.0	1.8
Bacterial feeders				
Rhabditis	80	1.5	0.7	0.6
Bunonema	24	0.4	0.2	0.2
Acrobeloides	1 057	19.4	20.0	17.9
Cervidellus	14	0.3	0.2	0.2
Teratocephalus	445	8.2	1.3	1.2
Euteratocephalus	35	0.6	0.1	0.1
Plectus parietinus	783	14.4	20.5	18.3
P. longicaudatus	159	2.9	3.4	3.0
Chronogaster	47	0.9	0.4	0.4
Wilsonema	87	1.6	0.9	0.8
Monhystera	135	2.5	0.4	0.4
Prismatolaimus	211	3.9	1.8	1.6
Achromadora	2.2	0.04	0.1	0.1
Alaimus	0.5	0.01	0.003	0.003
Miscellaneous feeders				
Eudorylaimus	294	5.4	20.9	18.6
Aporcelaims	56	1.0	20.4	18.2
Dorylaiminae odeff.	29	0.5	5.4	4.8
Nematoda tot	5 380		112.0	

Table 8. Number of nematodes belonging to different feeding groups in different soil layers in Ih VA. Figures show number of animals g^{-1} dry soil, R/F Root/fungal feeders, B Bacterial feeders, M Miscellaneous feeders (omnivores).

Month	S-layer			FH-layer 0-2.6 cm			Mineral soil M_1, 2.6-5.9			Mineral soil M_2, 5.9-10 cm		
	R/F	B	M	R/F	B	M	R/F	B	M	R/F	B	M
1974												
June	39	65	6	26	33	5	5.5	5.4	1.3	5.4	5.4	1.3
July	118	166	51	147	174	11	2.2	9.2	1.3	1.8	2.7	0.6
Aug.	101	116	22	70	116	18	4.4	7.5	0.6	9.0	13.0	0.9
Sept.	355	365	42	259	253	47	6.8	8.6	8.4	2.0	5.9	1.2
Oct.	176	221	50	247	166	44	6.7	9.5	0.8	6.8	3.0	0.5
Nov.	206	670	169	193	328	13	4.1	23.4	0.5	5.5	11.0	1.8
Dec.	368	658	90	485	268	46	23.2	12.7	0.2	6.5	9.3	0.8
1975												
Feb.	147	245	41	343	564	32	7.5	14.0	2.1	18.8	7.3	0.7
Apr.	161	345	18	190	519	45	4.5	18.1	3.7	8.8	21.9	2.7
May	67	183	28	71	132	11	4.9	10.8	3.2	6.0	4.8	0.3
June	86	183	5	68	68	14	14.6	10.2	0.4	12.1	5.5	0.4
Summer	86	116	26	81	108	11	4.0	7.4	1.1	5.4	7.0	0.9
Autumn	246	419	87	233	249	35	5.9	13.8	3.2	4.8	6.6	1.2
Winter	258	452	66	414	416	39	15.4	13.4	1.2	12.7	8.3	0.8
Spring	114	264	23	131	326	28	4.7	14.5	3.5	7.4	13.4	1.5
Annual mean	176	313	50	215	275	28	7.5	12.3	2.3	7.6	8.8	1.1
Rel. prop. %	32.7	58.0	9.3	41.5	53.1	5.4	33.9	55.7	10.4	43.4	50.3	6.3

Table 9. Number and biomass of different feeding groups of nematodes per m^2 in the uppermost 10 cm of the soil in Ih VA. Figures show number of animals in thousands m^{-2} (No 10^3) and dry weight biomass in mg m^{-2} (Biomass).

Month	Root/fungal feeders		Bacterial feeders		Miscellaneous feeders	
	No 10^3	Biomass	No 10^3	Biomass	No 10^3	Biomass
1974						
June	415	5.5	702	6.3	142	20.7
July	1 184	11.2	1 727	30.2	246	40.3
Aug.	1 096	11.2	1 712	27.1	195	14.1
Sept.	2 317	19.8	2 533	47.3	680	49.7
Oct.	2 138	9.9	1 881	34.6	412	26.4
Nov.	1 807	11.9	4 030	81.4	307	35.9
Dec.	4 129	23.2	3 573	67.5	474	59.6
1975						
Feb.	2 605	22.9	5 579	62.3	386	39.0
Apr.	2 039	19.9	5 179	81.2	594	122.4
May	962	11.8	1 617	33.0	218	28.4
June	1 213	8.8	1 457	21.3	97	20.4
Summer	898	9.3	1 380	21.2	194	25.1
Autumn	2 088	13.9	2 815	54.5	466	37.3
Winter	3 368	23.0	4 576	64.9	430	49.3
Spring	1 501	15.9	3 398	57.1	406	75.4
Annual means	1 964	15.5	3 042	49.4	374	46.8
Ratio max/min	9.9	4.2	7.9	12.9	7.0	8.7
Rel.prop. %	36.5	13.9	56.5	44.2	7.0	41.9

Table 10. Weight-class division and relation between live weight biomass and respiration (at 20°C) used for estimation of respiratory activity of field population of nematodes and rotifers. The weight/respiration regression described by Klekowsky et al (1972) was used.

Weight class	Class borders µg lw	Mean weight µg lw	Mean respiration $\mu l \cdot 10^{-5} ind^{-1} h^{-1}$	Wt spec. resp. $ml\ O_2 g^{-1} h^{-1}$
1	$(0 - 0.3) \cdot 10^{-3}$	$0.15 \cdot 10^{-3}$	0.2471	16.47
2	$a \cdot 10^{-3}$	$c \cdot 10^{-3}$	0.7165	10.94
3	$b \cdot 10^{-3}$	$d \cdot 10^{-3}$	1.642	7.89
4	$a \cdot 10^{-2}$	$c \cdot 10^{-2}$	3.760	5.71
5	$b \cdot 10^{-1}$	$d \cdot 10^{-1}$	8.616	4.14
6	$a \cdot 10^{-1}$	$c \cdot 10^{-1}$	19.73	3.00
7	b	d	45.25	2.17
8	a	c	103.6	1.57
9	$b \cdot 10$	$d \cdot 10$	237.3	1.14
10	$a \cdot 10$	$c \cdot 10$	543.5	0.83

a = 0.3162-0.9998 µg   c = 0.6580 µg

b = 0.1000-0.3161 µg   d = 0.2081 µg

Table 11. Weight-class composition and individual mean live weight-values of different feeding groups of nematodes sampled in Ih VA. Figures show relative frequency (%) on each sampling occassion.

Root/fungal feeders

Weight class	1974 June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1975 Feb.	April	May	June
3	12.3	4.4	3.7	3.6	5.8	5.0	2.5	6.0		2.6	6.4
4	35.4	35.6	41.1	16.7	30.6	50.0	28.3	34.9	44.2	25.0	42.1
5	16.9	21.1	30.8	46.4	43.8	25.0	45.0	28.9	31.4	35.5	31.0
6	18.5	25.6	14.0	19.0	13.2	1.7	15.8	20.5	12.8	25.0	11.9
7	13.8	5.6	8.4	10.7	5.0	16.7	6.7	4.8	10.5	7.9	7.1
8	3.1	7.8	1.9	3.6	1.7	1.7	1.7	4.8	1.2	3.9	1.6
Mean live wt μg	0.07	0.05	0.05	0.04	0.02	0.03	0.03	0.04	0.05	0.06	0.04

Bacterial feeders

Weight class	1974 June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1975 Feb.	April	May	June
1								1.1			
3	1.1		0.7		2.7		0.9	3.4	1.5		3.0
4	2.3	4.0	3.3	0.9	3.5		6.3	9.0	6.6	1.7	22.0
5	8.0	5.6	17.8	5.1	9.7	7.7	3.6	29.2	17.2	2.6	33.0
6	64.4	69.0	70.4	75.2	61.9	78.3	71.4	49.4	62.6	77.6	31.0
7	14.9	19.8	2.6	10.3	12.4	11.2	12.5	7.9	6.6	11.2	6.0
8	9.2	1.6	5.3	8.5	8.8	2.8	3.6		5.6	6.0	3.0
9					0.9		1.8			0.8	2.0
Mean live wt μg	0.05	0.09	0.08	0.09	0.09	0.10	0.09	0.06	0.08	0.10	0.07

Miscellaneous feeders

Weight class	1974 June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1975 Feb.	April	May	June
5			3.8								
6	23.5	4.3	15.4	25.9	31.3		10.0		5.9	13.0	33.3
7	41.2	52.2	53.8	40.7	37.5	45.5	40.0	25.0	41.2	39.1	44.4
8	29.4	34.8	15.4	22.2	25.0	36.4	20.0	50.0	17.6	30.4	11.1
9		4.3	11.5	11.1	6.3	18.2	20.0	25.0	35.3	17.4	
10	5.9	4.3					10.0				11.1
Mean live wt μg	0.73	0.82	0.36	0.37	0.32	0.59	0.63	0.51	1.03	0.65	1.05

Table 12. Weight-class composition and individual mean live weight-values of nematodes sampled in Ih VA. Figures show relative frequency (%) on each sampling occasion.

Weight class	1974 June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1975 Feb.	April	May	June
1								0.6			
3	5.3	1.7	1.8	1.3	4.0	1.4	1.7	4.5	1.0	0.9	4.7
4	14.8	15.5	17.2	6.6	16.4	14.0	16.9	21.0	16.9	9.8	31.9
5	10.7	10.9	21.4	19.7	25.6	12.1	24.0	28.4	20.3	14.0	30.6
6	42.6	46.4	44.2	48.7	36.4	52.8	41.3	34.7	45.2	52.1	20.9
7	17.2	17.6	9.5	14.0	10.4	14.5	10.7	6.8	9.6	13.0	8.1
8	8.9	7.1	4.9	8.3	6.4	4.2	3.3	3.4	5.0	7.9	2.6
9	0.6	0.4	1.1	1.3	0.8	0.9	1.7	0.6	2.0	2.3	0.9
10		0.4					0.4				0.4
Mean live wt μg	0.13	0.13	0.09	0.11	0.08	0.11	0.09	0.07	0.14	0.13	0.09

Table 13. Respiratory metabolism in different faunal grops in Ih VA. Figures show oxygen consumption in $1\ m^{-2}h^{-1}$. (R/F) Root/fungal feeding nematodes. (Bact) Bacterial feeding nematodes. (Misc) Omnivorus nematodes (miscellaneous feeders). (Nem) All nematodes. (Rot) Rotifers. (Tard) Tardigrades. (Tot) Total metazoan microfauna.

Month	R/F	Bact.	Misc.	Nem.	Rot.	Tard.	Tot.
1974							
June	29	90	53	172	175	7	354
July	117	224	121	462	58	46	565
Aug.	69	186	68	322	55	3	380
Sept.	192	356	242	790	89	9	888
Oct.	50	113	53	216	31	7	253
Nov.	33	130	42	206	65	5	275
Dec.	57	109	73	239	28	9	276
Jan.	32	61	40	133	16	5	154
Feb.	6	14	7	27	4	1	32
March	4	13	7	24	5	1	31
April	4	16	10	29	7	2	38
May	35	101	44	180	36	24	240
June	56	118	38	212	118	14	344

Table 14. Number, biomass and respiratory metabolism of different animal groups in Ih VA. Figures for number and biomass show annual mean values m^{-2}. Figures for metabolic activity show total annual values m^{-2} expressed as ml oxygen consumed, Kcal energy dissipated and amount of carbon emitted as carbon dioxide. The last column gives the annual weight specific energy dissipation.

Category	Number$\cdot 10^3$	Biomass mg dw	Metabolic activity ml O_2	Kcal	mg C	Kcal/g live wt
Root/fungal feeding nematodes	1 964	16	458	2.2	196	27.4
Bacterial feeding nematodes	3 042	49	1 031	4.9	442	20.1
Omnivorus nematodes	374	47	555	2.7	238	11.3
Nematoda total values	5 380	112	2 044	9.8	876	17.4
Rotatoria	578	37	415	2.0	178	10.7
Tardigrada	60	13	87	0.4	37	8.1
All groups	6 018	162	2 546	12.2	1 091	

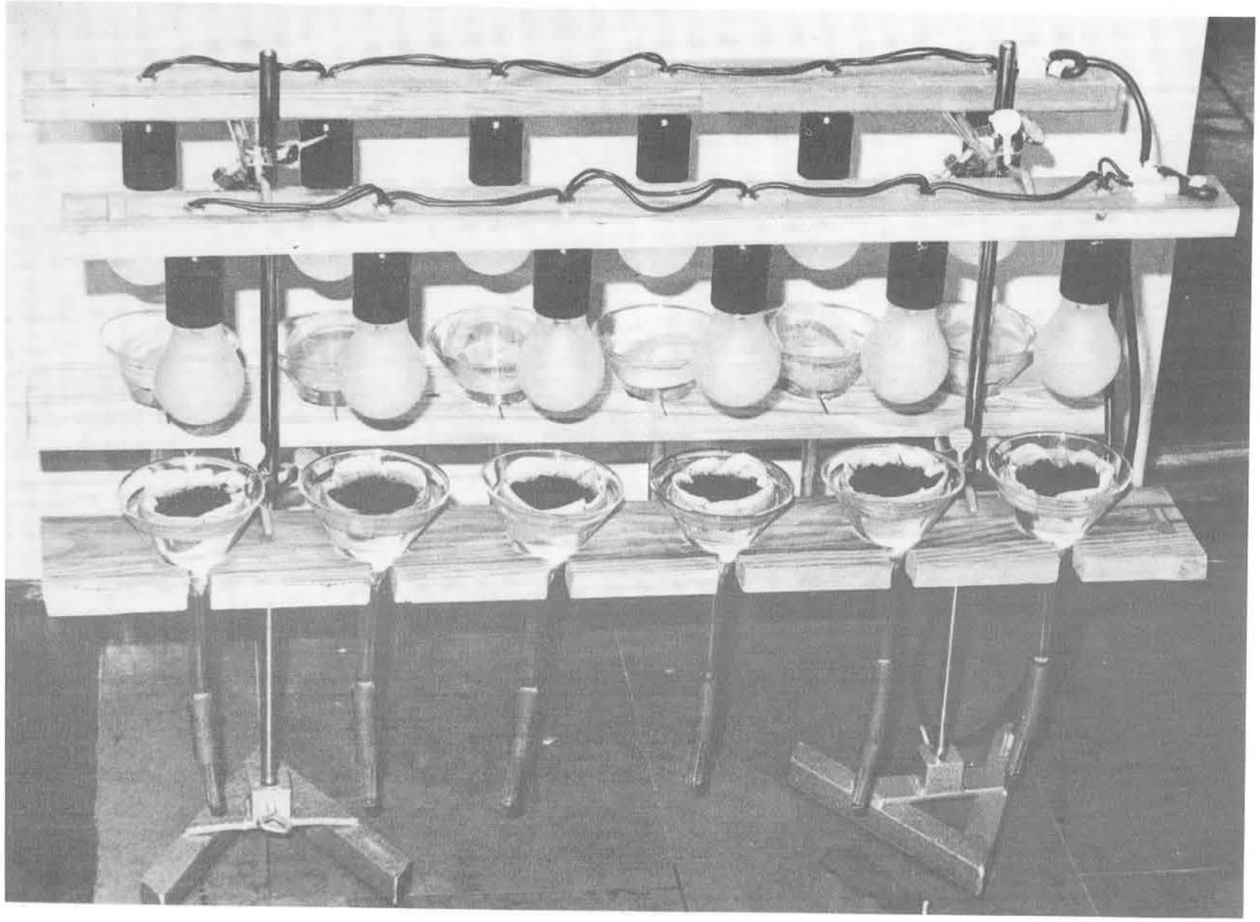
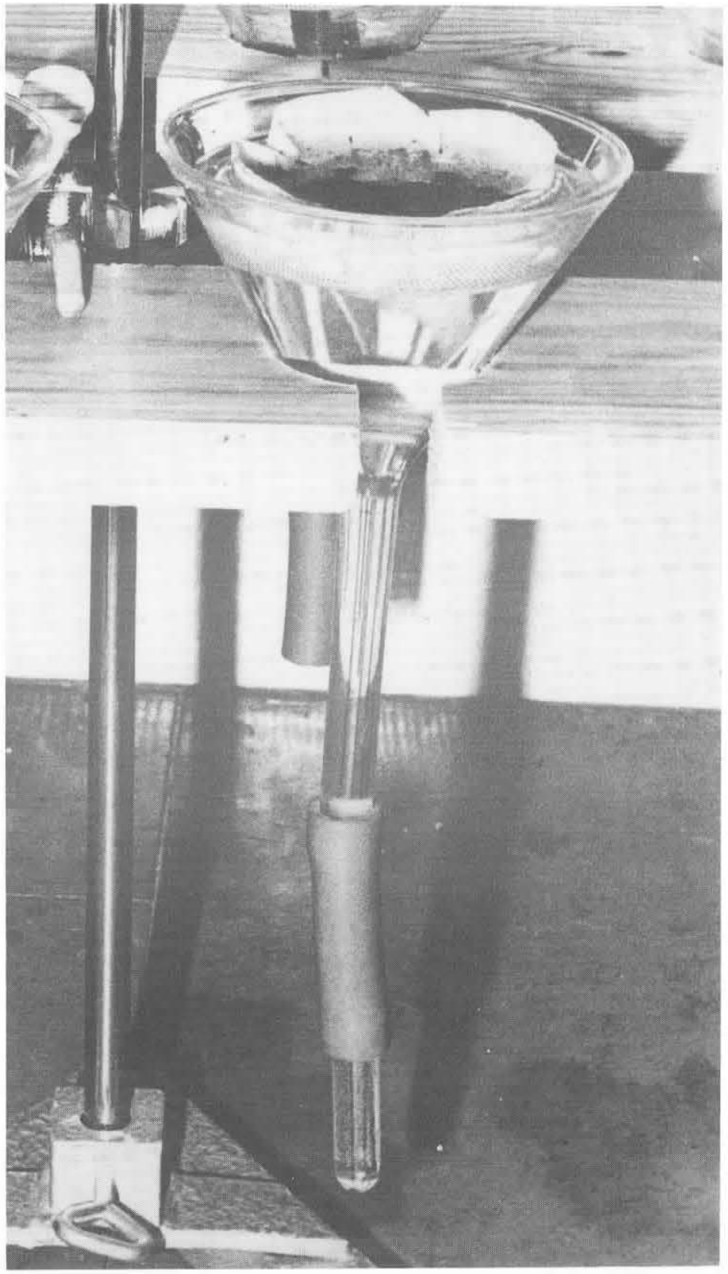


Figure 1. Apparatus for quantitative extraction of nematodes, rotifers and tardigrades from small soil samples



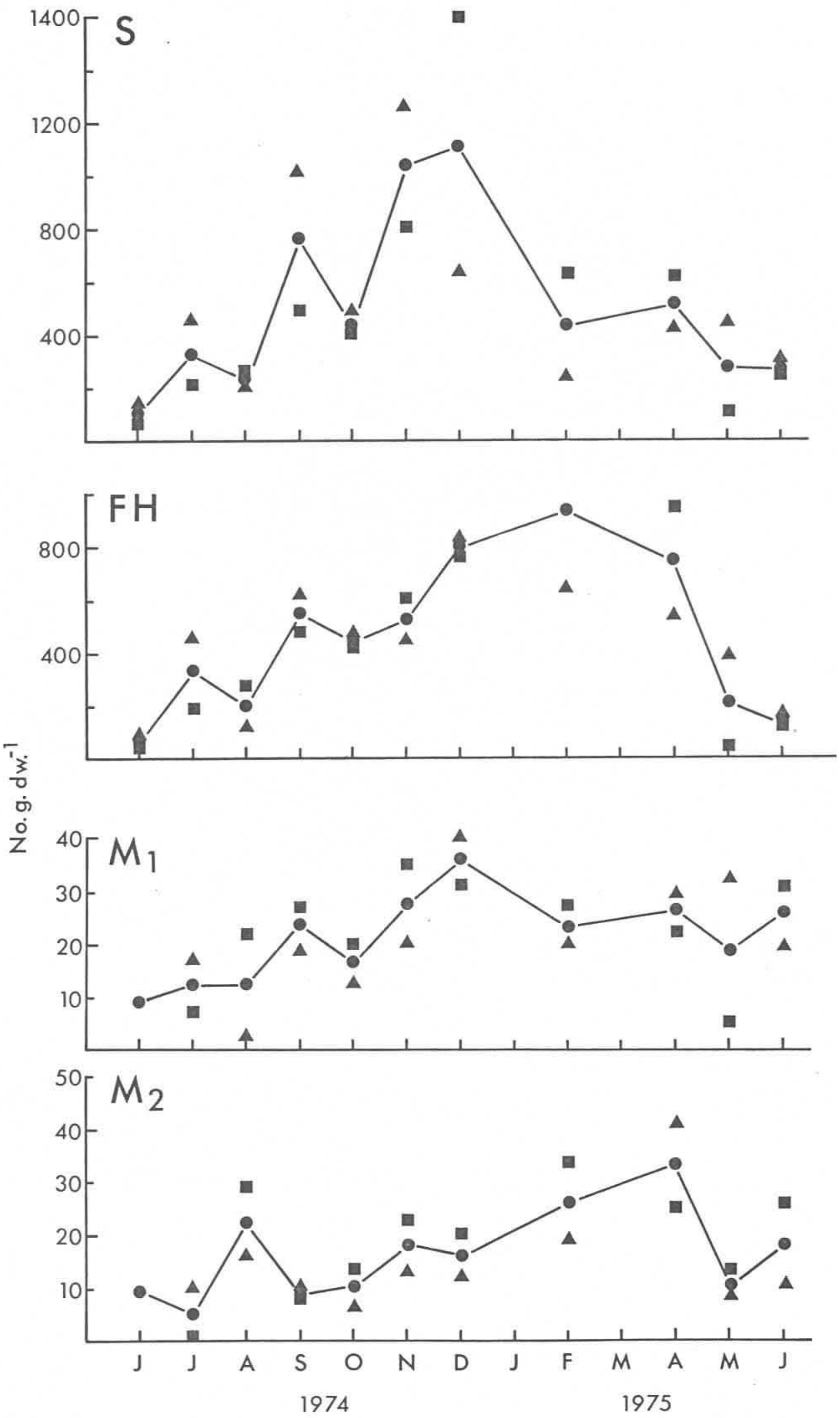


Figure 2. Number of nematodes per gram soil (dw) in different soil layers in Ih VA. (S) Litter layer, (FH) Humus layer. (M_1) Uppermost 3.3 cm and (M_2) the following 4.1 cm of the mineral soil. Squares and triangles represent pooled values from three sampling stations each.

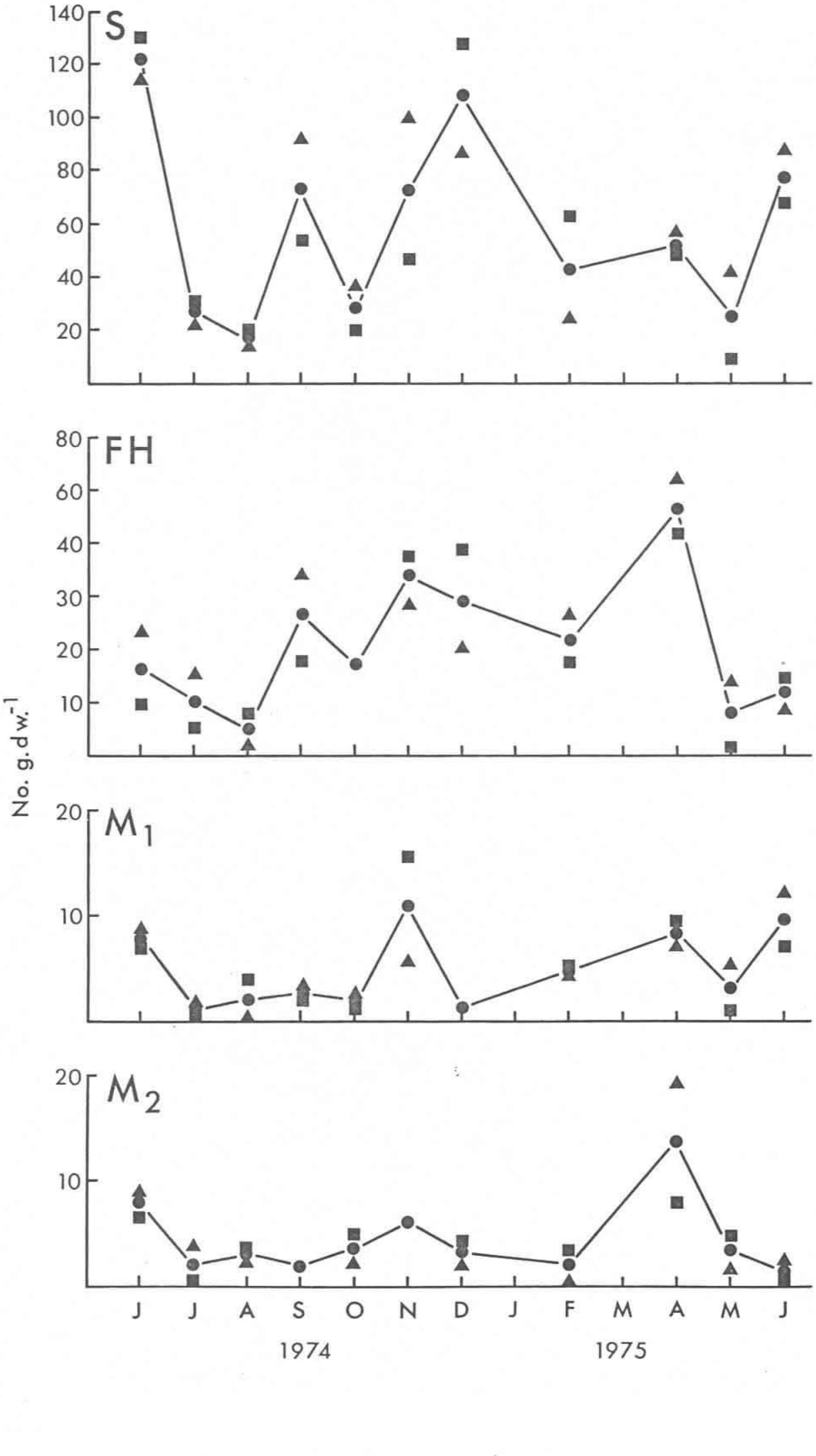


Figure 3. Number of rotifers per gram soil (dw) in different soil layers Abbreviations as in Fig. 2.

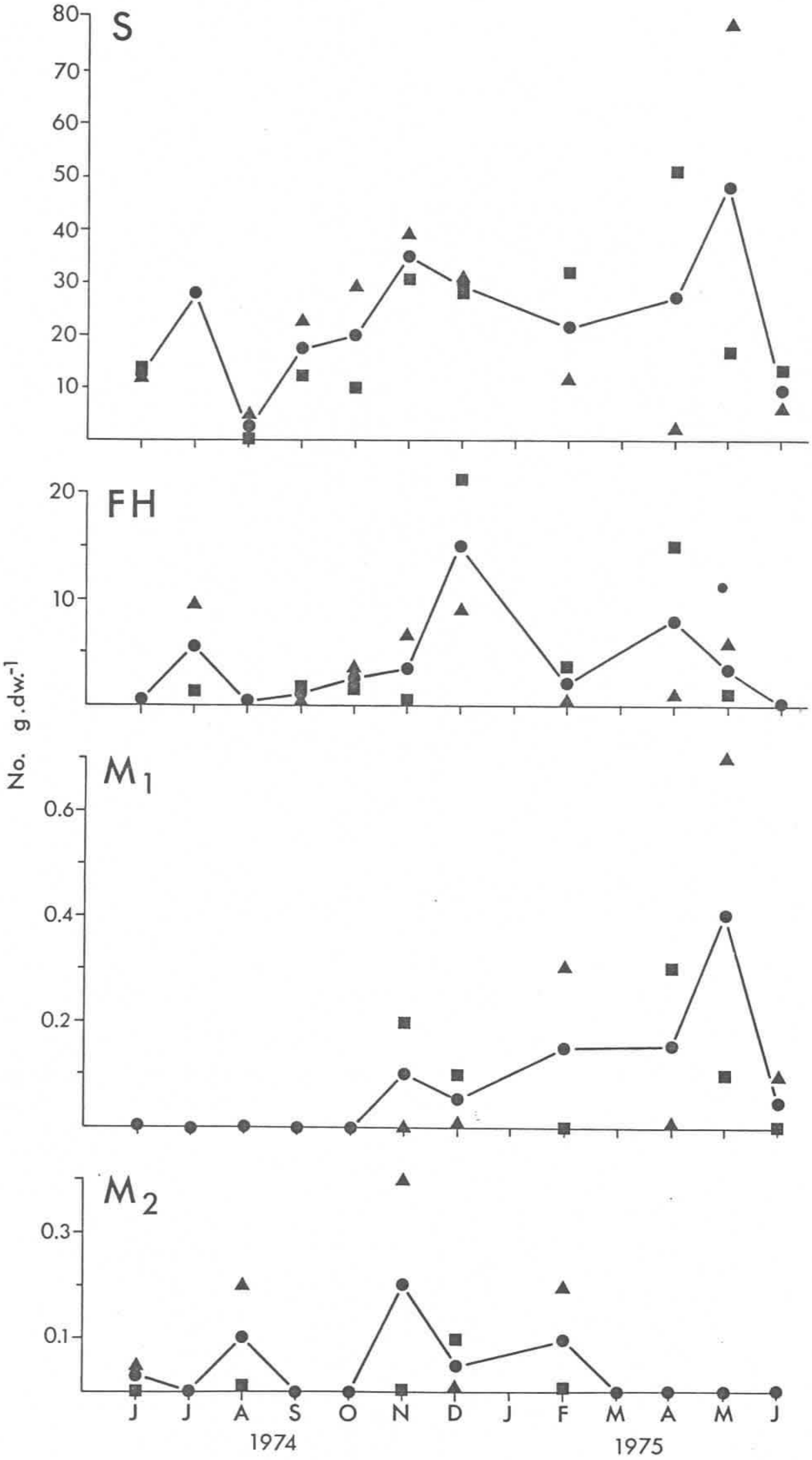


Figure 4. Number of tardigardes per gram soil (dw) in different soil layers. Abbreviations as in Fig. 2.

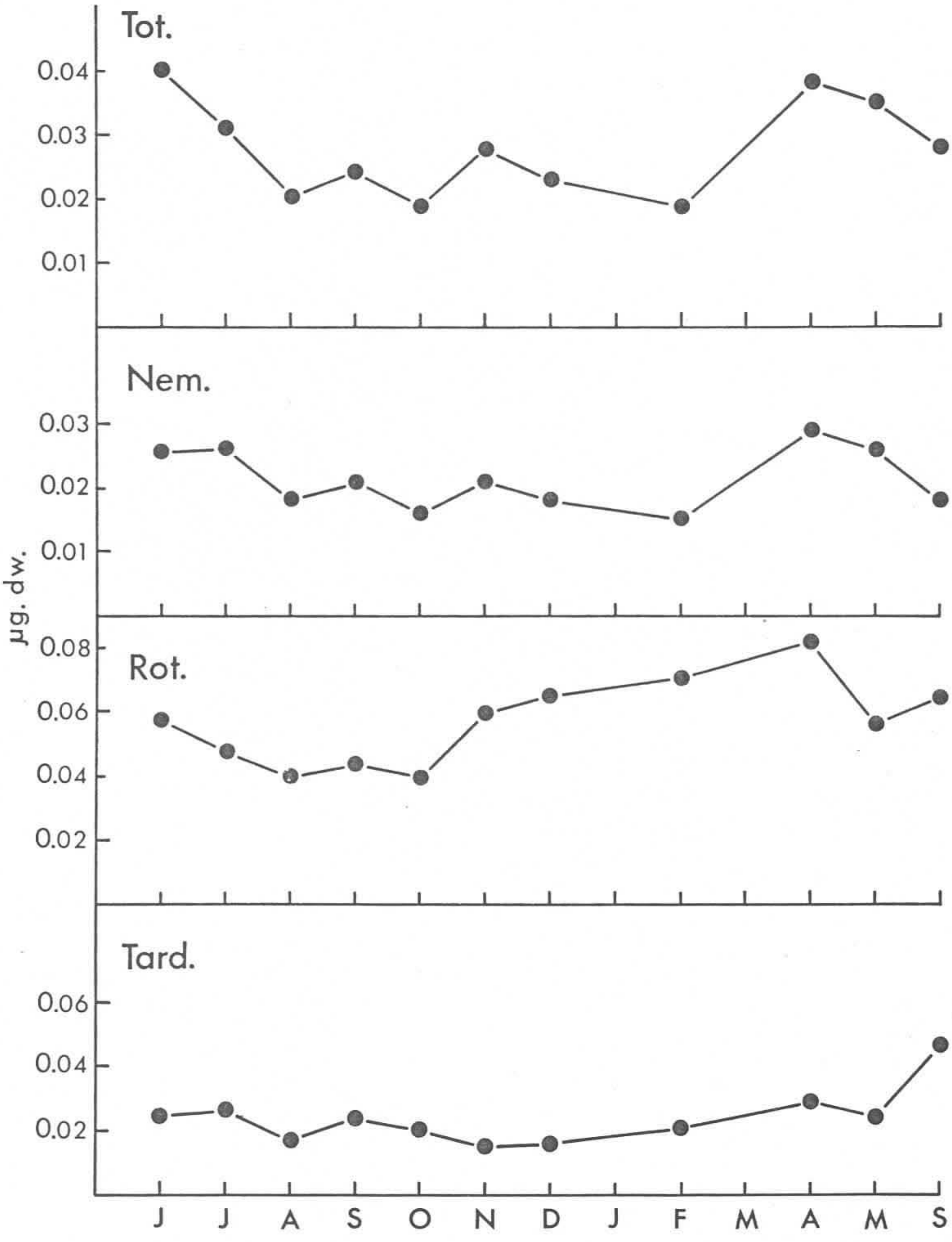


Figure 5. Individual mean dry weight biomass. (Tot.) Total metazoan microfauna. (Nem.) Nematoda. (Rot.) Rotatoria. (Tard.) Tardigrada. The values are obtained from animals from all four examined soil layers, integrating specific values of different species and genera.

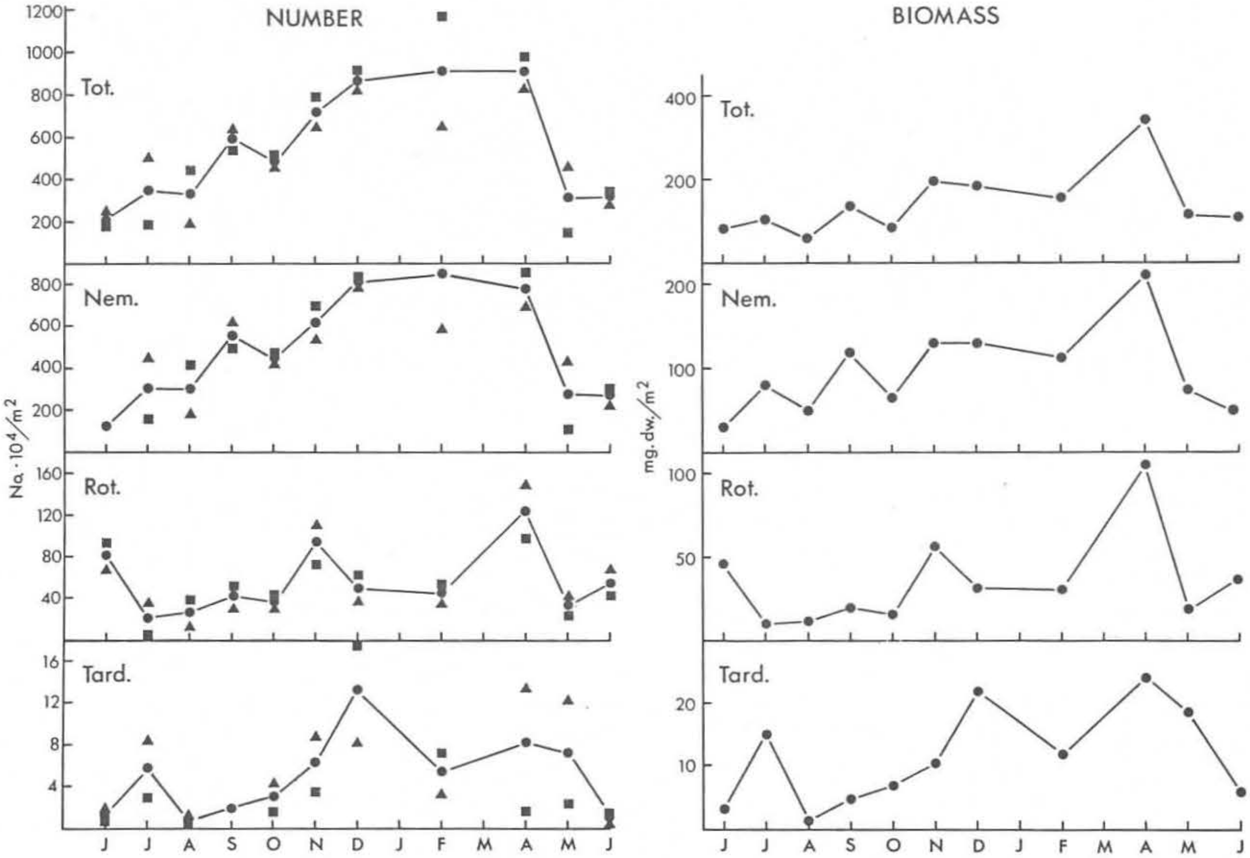


Figure 6. Number ($\cdot 10^4$) and biomass (g dw) per m^2. Abbreviations as in Fig. 5.

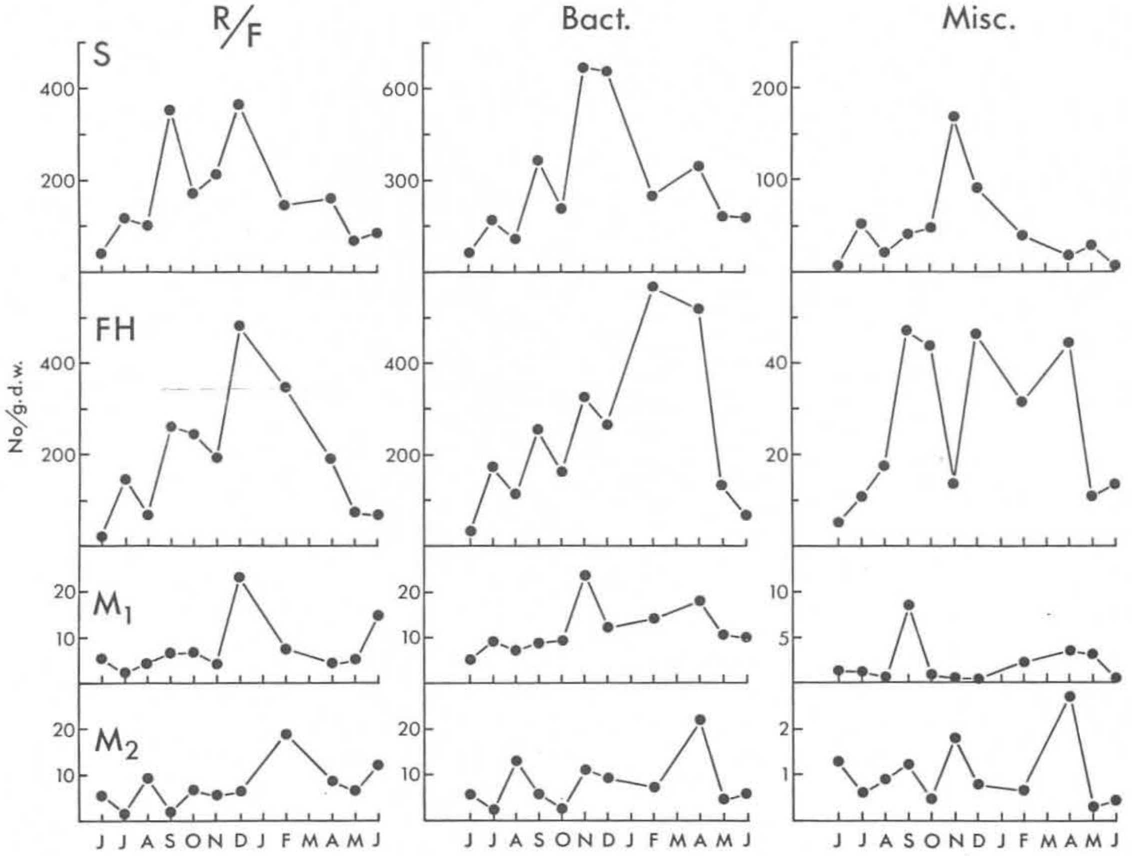


Figure 7. Number of nematodes belonging to different feeding groups per gram soil (dw). (R/F) Root/fungal feeders. (Bact.) Bacterial feeders. (Misc.) Miscellaneous feeders.

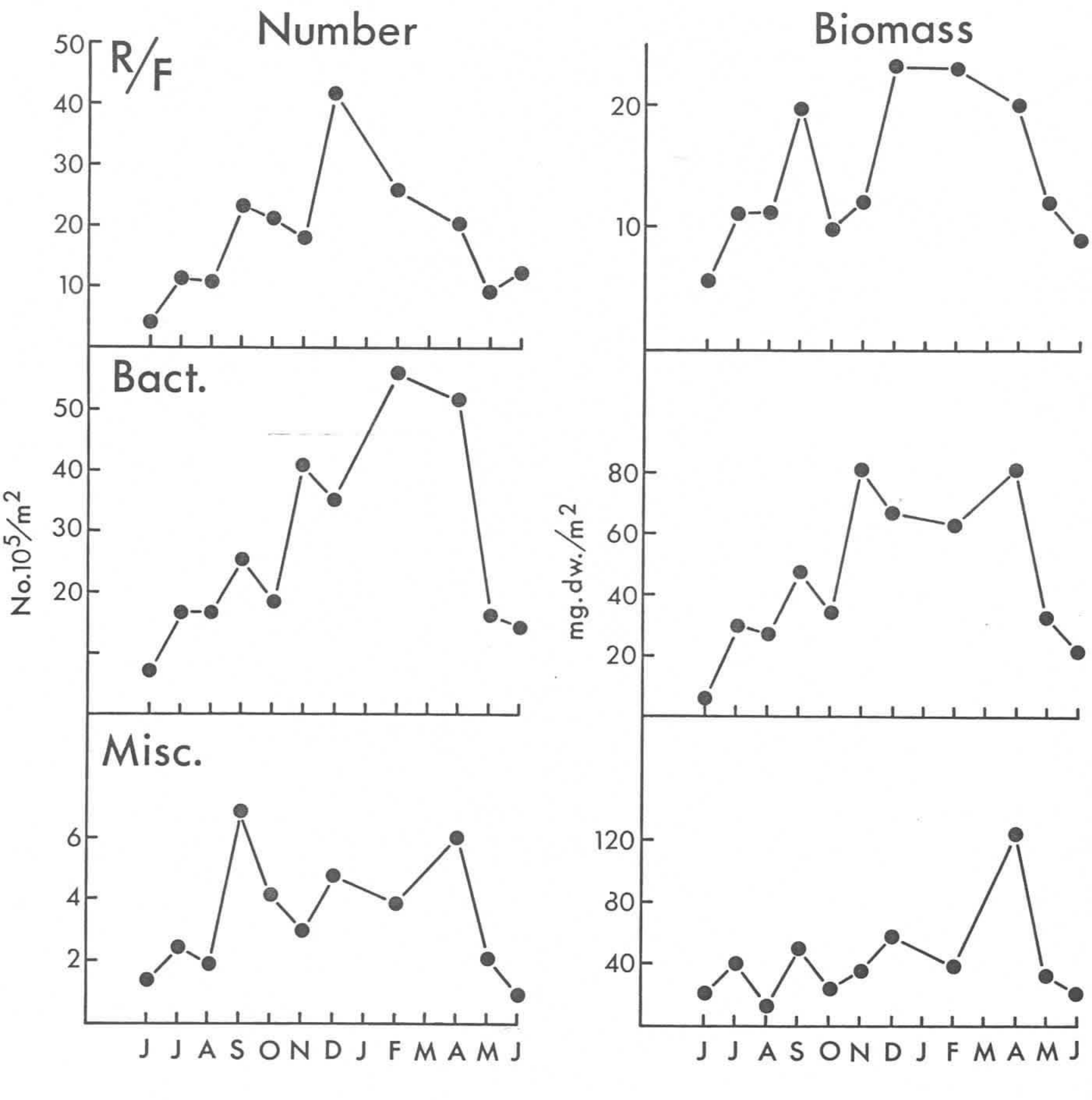


Figure 8. Number (10^5) and biomass (mg dw) of nematodes belonging to different feeding groups per m^2. Abbreviations as in Fig. 7.

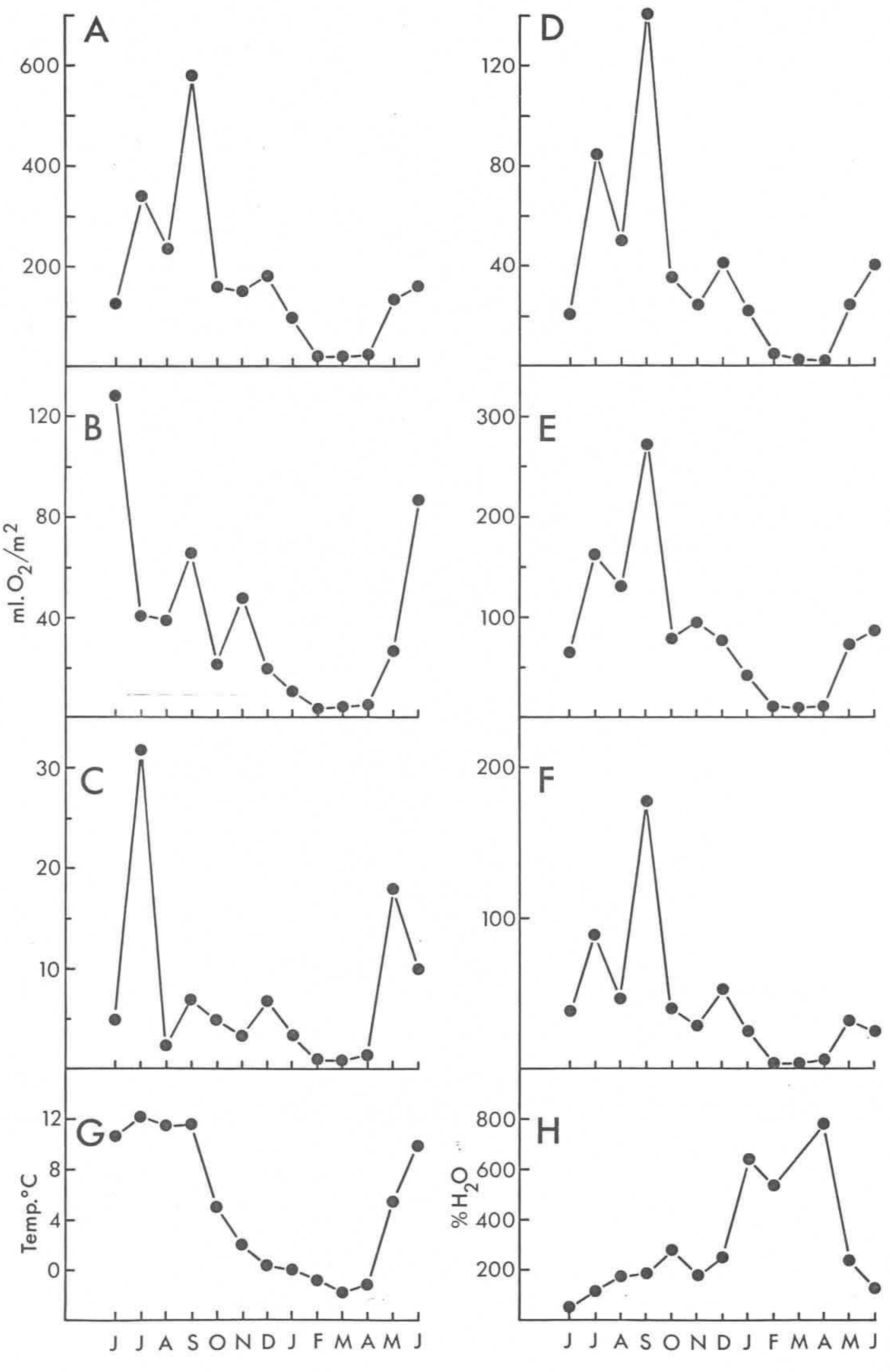


Figure 9. Oxygen consumption (ml O_2/m^2) of different faunal groups. (A) Nematoda. (B) Rotatoria. (C) Tardigrada. (D) Root/fungal feeding nematodes. (E) Bacterial feeding nematodes. (F) Omnivorus nematodes (miscellaneous feeders). (G) Mean soil temperature at a depth of 5 cm. (H) Water contents (% of dry weight) in the FH-layer.

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